**WALTER AND ANDRÉE DE NOTTBECK FOUNDATION**
**SCIENTIFIC REPORTS**
**No. 48**

# Exploring the diversity patterns of benthic diatoms along environmental, spatial and temporal gradients in the Baltic Sea

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*Academic dissertation in Geography*
*to be presented for public examination with the permission of*
*the Faculty of Science of the University of Helsinki,*
*in Banquet Room 303,*
*Unioninkatu 33,*
*on November20th, 2020, at 12 noon.*

**Helsinki 2020**

The thesis is based on the following publications, which are referred to in the text by their roman numerals. While publications I-V are published original research articles, the second publication in the list is a popularized version of publication I. It has been accepted for publication in *Frontiers for Young Minds*, which is a scientific, peer-reviewed journal aimed for children and teenagers. This popularized version has been included in the thesis, because I believe that communicating the importance of biodiversity to a broader public is crucial, and such popularized articles may reach both children and adults including politicians and decision makers, who need plenty of help from researchers to make good decisions on how to manage ecosystems in the best possible way.

**I.** **Virta, L.**, Gammal, J., Järnström, M., Bernard, G., Soininen, J., Norkko, J. & Norkko, A. 2019. The diversity of benthic diatoms affects ecosystem productivity in heterogeneous coastal environments. *Ecology* 100:9, e02765. *

With appendix: **Virta, L.** & Norkko, A. Do you like to breath? – Diatoms can help you with that! Accepted for publication in *Frontiers for Young Minds*.

**II.** **Virta, L.**, Soininen, J. & Norkko, A. 2020. Biodiversity loss threatens the current functional similarity of beta diversity in benthic diatom communities. *Microbial Ecology*, published online 8/2020. **

**III.** **Virta, L.** & Soininen, J. 2017. Distribution patterns of epilithic diatoms along climatic, spatial and physicochemical variables in the Baltic Sea. *Helgoland Marine Research* 71, 16. **

**IV.** **Virta, L.**, Soininen, J. & Norkko, A. 2020. Diversity and distribution across a large environmental and spatial gradient: evaluating the taxonomic and functional turnover, transitions and environmental drivers of benthic diatom communities. *Global Ecology and Biogeography*, published online 9/2020. *

**V.** **Virta, L.**, Soininen, J. & Norkko, A. 2020. Stable seasonal and annual alpha diversity of benthic diatom communities despite changing community composition. *Frontiers in Marine Science* 7, 88. **



**Authors' contributions to individual publications**

| | Paper I | Paper II | Paper III | Paper IV | Paper V |
|---|---|---|---|---|---|
| Study design | LV, AN, JN, JG, MJ, GB | LV, JS, AN | LV, JS | LV, AN | LV, AN, JS |
| Data collection | AN, JG, MJ, GB | LV, AN | LV | LV | LV |
| Laboratory analyses | LV, JG, MJ | LV | LV | LV | LV |
| Data analyses | LV | LV | LV | LV | LV |
| Manuscript preparation | LV with all authors | LV with all authors | LV with all authors | LV with all authors | LV with all authors |
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# Exploring the diversity patterns of benthic diatoms along environmental, spatial and temporal gradients in the Baltic Sea

Virta, L. 2020: Exploring the diversity patterns of benthic diatoms along environmental, spatial and temporal gradients in the Baltic Sea. W. and A. de Nottbeck Foundation Sci. Rep. 48: 1–40. ISBN 978-951-51-6772-9 (paperback), ISBN 978-951-51-6773-6 (PDF, http://ethesis.helsinki.fi)

During the ongoing rapid environmental change, different aspects of biodiversity and its effects on ecosystem functioning need to be resolved. A lot has already been learned regarding the value of biodiversity, but due to the complexity of natural environments many aspects are still unresolved, especially about the patterns and effects of microorganismal diversity in marine and brackish environments. This is surprising, given that microorganisms play key roles in many ecosystem functions and the marine microorganisms are estimated to, e.g., provide the majority of Earth's oxygen. To facilitate better understanding, studies conducted along large gradients and considering the functional diversity of communities can be useful. Large gradients provide insights into the variation of ecological patterns relative to the environment and can indicate the consequences of environmental change on community responses, and the functional diversity may describe the community characteristics and diversity-ecosystem functioning relationships more effectively than taxonomic diversity and allow the generalizations of results between organisms and ecosystems to be made.

In this thesis, biodiversity patterns of benthic diatoms, a highly diverse and productive microorganismal group in all aquatic systems, were resolved along different environmental, spatial and temporal gradients in the coastal ecosystems of the Baltic Sea. Being one of the world's largest brackish water ecosystems with a naturally strong gradient of salinity and climate and with a unique mixture of marine and freshwater species, the Baltic Sea provides an ideal platform for biodiversity research. Biodiversity patterns resolved here included analyzing the effects of benthic diatom diversity on ecosystem productivity, investigating spatial and temporal beta diversity patterns, i.e. the change in community composition between sites or sampling occasions, and examining the effects of environment on the distribution and diversity of diatoms. All studies were conducted as field studies to increase knowledge on real-world processes.

The results revealed some significant new insights and showed that the diversity, especially functional diversity, of benthic diatoms may set the lower boundary for ecosystem productivity. Thus, productivity could be high even when the diatom diversity was low, but high diatom diversity seemed to consistently support high productivity. This positive relationship may be due to several reasons, such as more complete resource use or the facilitative effect in diverse communities, or complex ecological interactions. However, the diversity of diatoms varied substantially among different habitats, highlighting the need to consider environmental heterogeneity and large environmental gradients in biodiversity research.

Spatial beta diversity studies conducted at different spatial scales indicated a general pattern: across steep environmental gradients, the taxonomic beta diversity was consistently high while the functional beta diversity remained considerably lower. This suggests that the ecosystem requirements for the functional characteristics of microphytobenthic organisms are highly similar in different environments, and that diatoms are able to meet these requirements in variable environments, which may indicate an insurance effect against environmental change. However, simulated species loss of communities significantly increased the functional beta diversity, suggesting that the deterioration of diversity may

decrease resilience, and thus emphasizing the importance of biodiversity for the stable functioning of benthic ecosystems.

Despite some similarities in the environmental drivers of diatom communities in different environments, environmental variables controlling the communities varied between and within gradients. Thus, the effect of environment on communities seems to be context-dependent and variable between regions, which emphasizes the need for large-gradient studies and the consideration of region-specific differences in, e.g., environmental management and conservation efforts.

The seasonal and inter-annual variation in the composition and diversity of communities was investigated along a temporal gradient of two years. The taxonomic and functional composition of communities changed significantly between seasons and years, while diversity remained fairly stable. This refers to either an ample seed bank, i.e. locally occurring resting stages of species, or a large regional species pool and effective dispersal of species, which rescue the populations. However, diversity decreased during an exceptionally warm winter with a short ice-cover duration, which may suggest that climate warming affects the diversity of benthic communities.

To conclude, this thesis has increased the knowledge on the diversity and importance of benthic diatoms in complex real-world environments. Some of the diversity patterns were general and non-dependent of spatial scale, whereas others were highly variable between regions and gradients. The results emphasize the need to consider the effect of benthic diatoms when modelling and designing the management of coastal areas, and indicate the usefulness of studies with environmentally and spatially large gradients for the understanding of diversity patterns in natural ecosystems.

CONTENTS

# 1. INTRODUCTION

## 1.1. Biodiversity, and diatoms as important components of aquatic ecosystems

Biodiversity describes the variability of organisms and encompasses all levels of variation from the genetic to species level and finally up to landscape and biome level. It affects all kinds of ecosystem functions, such as productivity (Hector et al. 1999), nutrient cycling (Hooper & Vitousek 1998), and stability (Girvan et al. 2005), as well as services that ecosystems provide to humans, such as food production or recreational values (Holmlund & Hammer 1999). During the current human induced global change and the consequent extinction wave, biodiversity has received increasing attention among scientists and general public, and a considerable amount of biodiversity research has been conducted in order to understand how and why biodiversity matters. A lot has already been learned, but due to the immense complexity of natural ecosystems, much still remains unclear and unexplored. While terrestrial ecosystems have been well represented in biodiversity studies, research on marine and brackish realms has lagged behind (Hooper et al. 2005), which has compromised the effective management of these systems. During the past few years, the number of studies on marine and brackish biodiversity has increased (e.g., Rapacciuolo et al. 2019; Lazzari et al. 2020), but most of the studies have, so far, been controlled experiments with limited duration, small spatial scale and homogeneous environments (Snelgrove et al. 2014; Gamfeldt et al. 2015). Although experiments can offer useful insights into the different aspects of biodiversity, they rarely capture the vast diversity, complexity and scale of natural marine ecosystems (Thrush et al. 2012). Thus, field studies, such as the ones presented in this thesis, are needed to deepen the understanding on the real-world biodiversity and its implications for ecosystem functioning at different scales.

Biodiversity can be described in several ways: in terms of the number of units, e.g. species, the evenness of their distribution, interactions between them, their genome, or differences in their functional traits (Hooper et al. 2005). Although taxonomic species richness is still the most common proxy for the diversity of a community (Torma et al. 2019), functional traits, such as morphology or dispersal mode, which are defined to influence ecosystem properties or species' responses to the surrounding environment (Hooper et al. 2005), can be more effective than species identities in describing the characteristics of the community and in showing the relationship between the diversity of the community and the functioning of the ecosystem (Chapin et al. 2000; Ceulemans et al. 2019). Furthermore, the concept of functional traits can be applied to all kinds of organisms and ecosystems and, thus, allows generalizations to be made (Violle et al. 2007; Wang et al. 2020).

Diatoms are one of the most diverse organism groups in aquatic ecosystems – in both benthic and pelagic realms –, with an estimated global species richness of >20 000 (Guiry 2012). They play important ecological roles, such as providing a food resource for meio- and macrofaunal grazers and contributing to biogeochemical cycling (Lohrer et al. 2004). Furthermore, they contribute ~20% of the total primary production on Earth (Nelson et al. 1995) (Fig. 1). Due to the high number of studies on the local distributions of diatoms, the environmental preferences of many species, especially those that live in freshwater ecosystems, are relatively well known (Weckström et al. 1997; Passy et al. 2004). Thus, they have been widely used as ecological indicators and in paleo-ecological studies for constructing past conditions. However, given the importance of diatoms, it is surprising how little is known about the effect of their diversity, especially functional diversity, on the functioning of ecosystems particularly in marine and brackish benthic environments. In this thesis, the functional diversity of diatoms is addressed and associated with general ecological patterns. The functional traits used here for the benthic diatoms indicate morphological characteristics of the communities, such as

the biovolume, height or mobility of species, and are closely related to ecosystem functioning. For example, benthic grazers depend on high-positioned and large diatom species, whereas low-positioned diatom species survive at low nutrient levels, where high-positioned and motile species no longer persist (Passy 2007). Thus, the inclusion of functional traits in diatom community analysis can lead to the understanding of fundamental ecological processes that would otherwise remain hidden.


Fig. 1. Diatoms and other aquatic microorganisms produce the majority of world's oxygen.

**1.2. Biodiversity change along environmental, spatial and temporal gradients**

Nature is heterogeneous and diversity patterns in natural ecosystems are often associated with different gradients, either spatial, environmental, or temporal (Huston 1994). Studies conducted along gradients and considering the natural heterogeneity of the ecosystem allow better understanding on how ecological patterns, such as variation in biodiversity, relate to environment (Thrush et al. 2000; Thrush et al. 2006; Hewitt et al. 2007). The oldest, most fundamental and probably the mostly widely studied gradient is the latitudinal diversity gradient, i.e., the decline of diversity with latitude (Willig et al. 2003), which has been shown to apply to all kinds of macro-organisms, in aquatic and terrestrial ecosystems (Hillebrand 2004). However, the effect of the latitudinal gradient and spatial distances in general, decreases with decreasing organism body mass, and is weak for microscopic, unicellular organisms, such as diatoms (Hillebrand 2004). This may be due to, e.g., effective dispersal, and suggests that the best predictor for unicellular diversity, instead of the spatial effect, is the variation and heterogeneity of the environment along gradients. However, gradients have often been ignored in community ecology (McGill et al. 2006), probably due to the complexity and constant spatial and temporal variation in physical and chemical gradients that considerably complicate the understanding of the gradients as the basis for biodiversity patterns.

Despite its challenges, the gradient approach can facilitate dimensions of community ecology that would otherwise remain unseen. For example, large gradients can provide insights into the consequences of environmental change on community responses (Thrush et al. 2006; Snelgrove et al.

2014), and gradients allow diversity studies from different perspectives, from alpha diversity, i.e. the diversity of local communities, to beta diversity, i.e. the change in species composition and diversity between sites, and finally to gamma diversity, i.e. the overall diversity within a region. Alpha diversity is a frequently studied diversity component, and the alpha diversity of different organisms has been shown to affect the functioning of local ecosystems (Loreau et al. 2001). Beta diversity, a much more rarely studied diversity measure, describes the dissimilarity in community structure along the gradient and may equal alpha diversity in importance for, e.g., conservation efforts, such as designing effective protective area networks or understanding processes that maintain diversity (Socolar et al. 2016). Thus, understanding beta diversity patterns is crucial for the management of ecosystems, but the underlying drivers of microorganismal beta diversity are still poorly studied and unclear (Martiny et al. 2006; Cao et al. 2016).

Brackish water ecosystems provide ideal gradients for studying different diversity measures. They are unique environments where peculiar and highly variable salinity conditions challenge the adaptation of organisms. The change in the diversity of organisms along the salinity gradient in brackish realms was first described by Remane (1934), who showed a minimum species diversity in intermediate salinities of ca. 6. His hypothesis, called the Remane curve, is due to the inability of freshwater or marine species to tolerate the intermediate salinities and the limited number of true brackish species, which stems from the paucity, small size and isolation of the world's brackish water basins and the consequently low speciation rate (Olli et al. 2019). The Remane curve has repeatedly been shown to hold true with the diversity of macro-organisms (Attrill & Rundle 2002; Zettler et al. 2014), but its validity with microorganismal diversity is disagreed (see Filker et al. 2019 for Remane opposing results, and Olli et al. 2019 for supporting results). Being one of the world's largest brackish environments, the Baltic Sea forms an effective gradient for biodiversity research; the restricted water exchange through narrow Danish Straits and the abundant river discharge from land lead to a natural salinity gradient, and the North-South dimension forms a climatic gradient from subarctic to temperate oceanic climate. Furthermore, the Baltic Sea is a young basin that has gone through major geological changes, which leads to continuously evolving biodiversity (Ojaveer et al. 2010). Due to, e.g., eutrophication (Bonsdorff et al. 1997; Vahtera et al. 2007), hypoxia (Conley et al. 2009) and other anthropogenic issues, but also the unique ecosystems and species adapted to the brackish conditions (Bergström et al. 2005), the Baltic Sea has been studied intensively. However, microorganisms have received less attention, especially along large gradients (but see Ulanova et al. 2009; Olli et al. 2019 for large gradient studies). This is surprising, because compared to macro-organisms whose diversity in the Baltic Sea is low due to the challenging salinity conditions and the young age of the basin, the diversity of microorganisms is high and enables the observation of different diversity patterns along the gradient.

### 1.3. Diversity-ecosystem productivity relationships

The relationship between biodiversity and ecosystem productivity has been studied widely in different ecosystems, such as terrestrial (Hector et al. 1999), freshwater (Aoki 2003) and marine (Aguirre & Marshall 2012). A common pattern found in the studies is that productivity either monotonically or unimodally increases with diversity, although flat, negative and random relationships have also been found. The varying results indicate that the effect of diversity on ecosystem productivity depends on the type of organisms, ecosystem and context. However, general mechanisms underlying the diversity-productivity relationship can be found. First of all, the theory of niche complementarity suggests that, due to differences in the resource requirements of functionally different species, the use of environmental resources is more complete in a taxonomically and functionally diverse community, thus leading to higher production (Hooper 1998). Secondly, diverse communities may be more productive,

because the biomass production of a certain species may increase due to the facilitative effect of other species, via resource enhancement or stress alleviation (Vandermeer 1989). Thirdly, the 'sampling effect' suggests that a highly diverse ecosystem is more likely to contain highly productive species than a species-poor ecosystem (Fridley 2001). And fourthly, the relationship may be controlled by complex ecological interactions, such as positive and negative feedback mechanisms (Weerman et al. 2010), resource availability limiting both diversity and productivity (Gross & Cardinale 2007), or herbivores having a nonlinear effect on productivity via top-down control of primary producers (Weerman et al. 2011).

So far, the majority of diversity-productivity studies has been experiments (Gamfeldt et al. 2015), and in determining the underlying reasons for the relationship, controlled experiments are indispensable. However, experiments often hold constant many environmental variables whose variation plays important roles in natural ecosystems. Thus, the results of experiments may be poorly extrapolatable to natural ecosystems especially in heterogeneous environments and on large scales, and more real-world studies are needed to improve the knowledge on the ecological relationships in complex natural environments (Gamfeldt et al. 2015; Gammal et al. 2019). Furthermore, despite the importance and huge diversity of microorganisms in all ecosystems, the effect of microorganismal diversity on ecosystem functioning is still understudied, and it is unclear whether the ecological behavior of microorganisms conforms to the rules that have been discovered for macro-organisms (Smith 2007).

# 2. AIMS OF THE THESIS

The overall aims of the thesis were to investigate the diversity of benthic diatoms at different environmental, spatial and temporal gradients in order to explore potentially general or varying patterns along the gradients, to study the effects of the diversity on ecosystem functioning, and to analyze the effect of the spatial observation scale on the diversity patterns. All the studies presented in the thesis were designed to increase knowledge of real-world processes and are, thus, based on field data. Papers I-IV represent studies with spatial gradients, in an increasing order of the gradient size. Paper V represents a study on a temporal gradient. It was important to include a temporal gradient study, because it validates the results of the other studies that were based on spatial snapshots.

The main questions were:

1. Does the taxonomic and functional diversity of benthic diatom communities affect the productivity of the ecosystem in a shallow coastal archipelago? (I)
2. What is the level of taxonomic and functional beta diversity of communities along environmental and spatial gradients? (II, III and IV)
3. Which local and regional factors control diversity at different environmental and spatial gradients? (I, III and IV)
4. How does alpha diversity vary along a seasonal and inter-annual temporal gradient? (V)

# 3. MATERIALS AND METHODS

## 3.1. Study areas

All the studies were conducted in different coastal areas of the Baltic Sea (Fig. 2). The study areas for papers I, II and V were located in southwestern Finland, where the effect of benthic diatom diversity on ecosystem productivity was studied in a coastal archipelago (I), whereas the spatial (II) and temporal (V) beta diversity of diatom communities were investigated along an estuarine gradient from a freshwater river to brackish archipelago and finally to the open sea. The study areas for papers III and

IV comprised larger areas of the Baltic Sea; the spatial beta diversity and the environmental drivers for the communities were studied along the entire Finnish (III) and Swedish (IV) coastline.

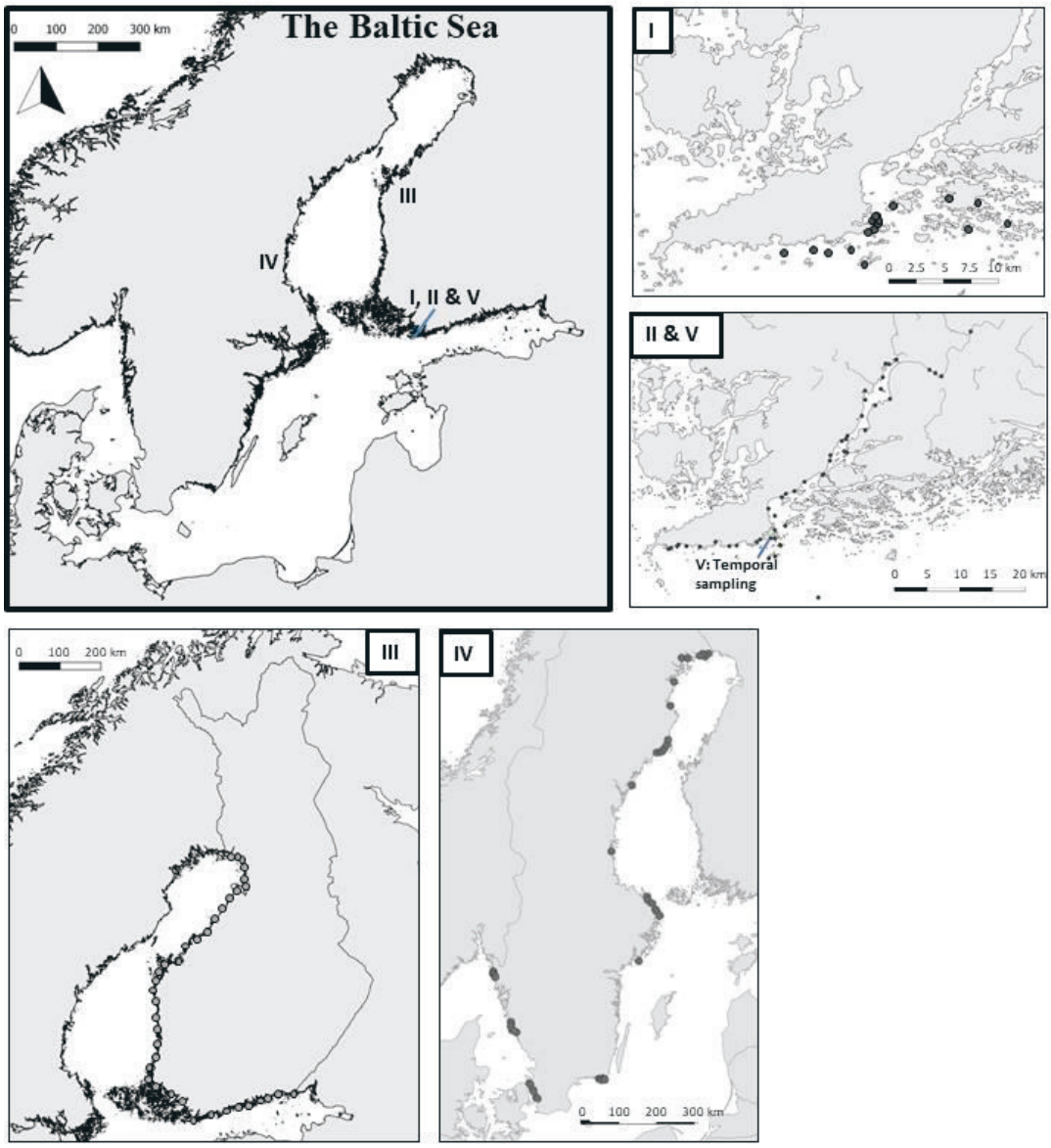


Fig. 2. Map of the Baltic Sea and sampling areas of papers I-V.

**Coastal archipelago in southwestern Finland (I)**

Sampling for paper I was conducted in an archipelago around the Tvärminne Zoological Station, close to the Hanko peninsula. The archipelago in this area is complex with a mixture of habitats from sheltered bays to exposed shores, bottom types varying from muddy/sandy to rocky, and aquatic vegetation ranging from bare sediment to dense plant/macroalgal cover (Gammal et al. 2019; Gustafsson & Norkko 2019). The salinity in this area is 5-6 and the archipelago area is generally shallow. The samples were collected from different kinds of habitats from shallow sedimentary bottoms (< 4 m).

**Gradient from a freshwater river through an estuary to the coastal archipelago and open sea in southwestern Finland (II and V)**

Sampling area for paper II was an estuarine environment with an exceptionally steep environmental gradient. Sampling covered the gradient from the freshwater river Karjaanjoki, which is a lowland river with slow currents; to the Pojo Bay estuary, where environmental conditions gradually change from freshwater to brackish with salinities increasing from 0.5 to 4.5, wind exposure increasing and water temperature decreasing; to the archipelago close to the Hanko peninsula, where salinity and wind exposure further increase; and to the open sea, where salinity is 5-7 and littoral communities are under constant and high wind-induced wave disturbance.

The main study area for paper V was a sheltered and shallow bay at the Tvärminne Zoological Station, where the temporal sampling was conducted. Due to the sheltered conditions, seasonal changes in the bay are pronounced with warm water temperatures during summers (occasionally over 20°C) and annually occurring ice cover during winters. For validating purposes, spatio-temporal samples were collected from the same estuarine gradient as in paper II.

**The Finnish coastline (III)**

Sampling for paper III covered the whole Finnish coastline, ca. 1300 km, along the Gulf of Bothnia and the Gulf of Finland. Several large rivers discharge to these coastal water bodies, which, along with the restricted water exchange between the Baltic Sea and the North Sea through the Danish Straits, results in decreasing salinity towards the North and East. Thus, biotic communities change from brackish dominance on the southwestern coast of Finland to freshwater dominance at the northern end of the Gulf of Bothnia and the eastern end of the Gulf of Finland. Rivers also increase the nutrient load of both gulfs, thus leading to eutrophication (Gustafsson et al. 2012).

**The Swedish coastline (IV)**

Sampling for paper IV was spatially largest and covered the whole Swedish coastline of ca. 2300 km between latitudes 55.73°N and 65.79°N and longitudes 11.17°E and 23.90°E. Sweden is located in the transition zone between the Baltic Sea and the North Sea, and climatically between continental and marine climates. Thus, many environmental variables, e.g. salinity and climate-related variables such as air and water temperature, follow a North-South and East-West gradient. Salinity increases from ca. 1 in the northeastern part of the coastline to ca. 28 in the southwestern part of the coastline, which results in biotic communities changing from freshwater to brackish and finally to marine species.

### 3.2. Field sampling and laboratory analyses

#### Paper I

78 samples were collected in August – September 2014 from 17 sites in a coastal archipelago. All sites were sedimentary soft bottoms, but variability of habitats within and across sites was high due to differences in, e.g., sediment characteristics, vegetation, and benthic fauna. At each site, scuba diving was used to collect 4-5 surface sediment samples with cutoff syringes along a transect of ca. 20 m. Also, an intact sediment core (15 cm of sediment and 15 cm of bottom water) was collected from the proximity of each surface sediment sample. Finally, the transects were videoed from the height of 50 cm above sea floor to allow the characterization of vegetation and stone cover around each sample location. In the laboratory, the surface sediment samples were used for diatom analysis (described below), and the characterization of sediment grain size by sieving, organic matter content by loss on ignition, and chlorophyll *a* concentration by spectrophotometry. Intact sediment cores were used for bottom-water nutrient analyses ($NO_2^-$, $NO_2^- + NO_3^-$, $NH_4^+$, $PO_4^{3-}$, and Si), and for the characterization of benthic macrofauna. For benthic macrofauna, species richness and species abundances were determined and macrofaunal species were classified into diatom inhibiting and facilitating species.

#### Papers II – V

For papers II – V, samples were collected from rocky substrata. For papers II – IV, emphasis was placed on conducting the sampling over a short period of time to minimize the potential for temporal variability.

For paper II, 51 samples were collected in June – July 2017 over a short time frame of nine days. Sampling sites along the freshwater-brackish estuarine gradient were rocky shores with a steep natural gradient and variability of environmental variables, such as salinity, exposure to waves, water temperature, and nutrients.

For paper III, samples were collected in July 2013 from 37 rocky shores in sheltered bays along the Finnish coastline. Distance between sampling sites was kept a constant of ca. 30 km, but large river mouths with ample nutrient loads were avoided.

For paper IV, sampling was conducted in August 2018. 52 samples were collected from rocky shores along the Swedish coastline (Fig. 3). To minimize the effect of terrestrial factors, sampling sites were chosen at far ends of peninsulas or islands, and close proximities of rivers were avoided. Furthermore, along the long spatial gradient of 2300 km, sampling was concentrated to areas, where changes in water chemistry are pronounced due to seafloor sills and consequent restricted water flow.

Fig. 3. Sampling sites along the Swedish coastline. Rocky shores at far ends of peninsulas and islands were chosen. Photographs represent the marine-freshwater gradient, top left corner featuring a site in Kattegat, top right corner a site in the Sound, and bottom left and right corners sites in the Bothnian Bay.

For paper V, temporal sampling (n=56) continued for ca. two years – 111 weeks – with two-week-intervals. The same sampling site, i.e. a sheltered bay, allowed the determination of temporal variation in communities, but sampling the same stones was avoided for at least two months, to allow the proper re-colonization of communities.

Diatom sampling in papers II-V was conducted following the modified recommendations of Kelly et al. (1998). At each site, five (III), ten (II and V) or twenty (IV) cobble-sized stones were randomly selected along the shore line from depths of 20-50 cm. The diatoms were collected by scraping 25 cm² of the surface of each stone with a toothbrush (II, III and V) or a sponge (IV), and the accumulated suspension was pooled into a composite sample. Despite this sampling method being generally accepted for diatom sampling, it has weaknesses. For example, it ignores the potentially large variance in the microphytobenthic communities and environmental conditions between microhabitats within each site. Thus, complementing this method with other sampling methods may bring more accuracy to the results of future studies.

Environmental variables were measured simultaneously with the diatom sampling. Local variables, namely water temperature (II – V), salinity/conductivity (II – IV), and pH (II – IV) were measured *in-situ*, and water samples were collected for nutrient analyses (II – IV). To estimate the stability of the substrate for benthic diatoms, dimensions of each stone (length × width × height) were measured (II, IV and V).

In the laboratory, water samples were used for the nutrient analyses of $NO_{2-} + NO_{3-}$, $PO_4^{3-}$, Si (II and IV) and total P (II) with an automated photometric analyzer, for the manual analyses of $NH_4^+$ (II and IV) and total N (II), and for the analysis of total P (III) following standard SFS-EN 1189.

In paper III, local environmental variables, namely total N, Si and O, were extracted from the data of the Finnish Environment Institute (2013, raster, spatial resolution 20 m) and interpolated with the Spatial Analyst tools of ArcGIS 10.2.1, Arcmap-applications (ESRI 2014).

### 3.3. Diatom analyses and trait characterization

In all papers, diatom samples were processed by boiling with hydrogen peroxide (30% $H_2O_2$) to remove organic material, and the cleaned diatoms were mounted on slides using Naphrax (Brunel Microscopes Ltd, United Kingdom). A phase contrast light microscope with a 1000× magnification was used to identify 300 (III) or 500 (I, II, IV and V) frustules per sample to the lowest possible taxonomic level, typically species level. Identification was based on Krammer and Lange-Bertalot (1986, 1988, 1991a, b), Snoeijs (1993), Snoeijs and Vilbaste (1994), Snoeijs and Potapova (1995), Snoeijs and Kasperovicienė (1996), and Witkowski (2000). Species counts were transformed into relative abundances, and taxonomic names were verified according to AlgaeBase (Guiry 2020). The diatom sample processing method used here is generally accepted for studies using benthic diatoms. However, it has a weakness of not being able to detect the absolute abundances of species, which is an important aspect for the diversity-ecosystem functioning relationships. Thus, complementing this method with other processing methods may be recommended in future studies, to find connections between diatom communities and ecosystem functions more effectively.

In papers I, II, IV and V, the functional characteristics of communities were accounted for by using functional traits. Diatom species were classified according to their size (biovolume classes: large > 1000µm³ / small < 1000µm³), mobility (mobile / non-mobile), type of attachment (adnate / pedunculate [which was further divided to pad-attached / stalk-attached] / non-attached), colonization (colonial / non-colonial), guild (low-profile / high-profile / motile / planktonic) (Rimet & Bouchez 2012), nitrogen-fixing abilities (nitrogen-fixer / non-nitrogen-fixer) (Passy 2007) (I, II, IV and V) and salinity preferences (freshwater / brackish / marine) (V). Each species in the community was categorized according to all 6-7 classifications, which resulted in numerous possible trait combinations. As the measure of trait composition of the community, the combination of traits of all the species present in the community was used. The identification of traits was completed with the help of above-mentioned literature, Snoeijs et al. (2002) and Diatoms of North America (2020).

### 3.4. Calculations of wind exposure and climatic variables

For papers II, III and IV, fetch, i.e., the distance over which wind can travel across open water, was calculated to account for the exposure of sampling sites to wind and wind-induced waves. In papers II and IV, fetch was calculated by measuring the distance from the exact study site to the closest shore, island or islet along 36 (IV) or 40 (II) lines that were 9° (II) or 10° (IV) apart from each other. This was done by means of a transparent circular disc (II) (Mason et al. 2018) or the ruler tool in Google Earth (Google) (IV). In paper III, the exposure of sampling sites was interpolated from the depth-attenuated

wave exposure model by the Finnish Environment Institute (2015; raster, spatial resolution 20 m), which is based on the Simplified Wave Model (Bekkby et al. 2008) and depth information.

In papers III and IV, the spatial gradient of the studies was large and, thus, climatic variables were used as explanatory variables for diatom communities. In paper III, July air temperature and July precipitation were derived from the data of the Finnish Meteorological Institute (representative of 1981-2000, grid, spatial resolution 10 m) (Pirinen et al. 2012). In paper IV, average annual temperature and precipitation were extracted from WorldClim global climate data (representative of 1950-2000, spatial resolution 1 km²) (Hijmans et al. 2005). For both papers, climatic variables for sampling sites were calculated using ArcGIS, Arcmap-applications (ESRI 2014 and 2018).

### 3.5. Statistical analyses

The main statistical methods used in papers I-V are presented in Table 1 and in the text below. All statistical analyses were conducted using R (R Development Core Team 2017, 2018 and 2019).

Table 1. Overview of the statistical methods used in papers I-V. ANOSIM = analysis of similarities, ANOVA = analysis of variance, dbRDA = distance based redundancy analysis, GAM = generalized additive model, GDM = generalized dissimilarity model, GLM = general linear model, LM = linear model, nMDS = non-metric multidimensional scaling, PCA = principal component analysis, RDA = redundancy analysis, SEM = structural equation model, SIMPER = similarity percentages test, TBI = temporal beta diversity index

| Paper | Spatial scale | Community characteristics | Response variables | Explanatory variables | Statistical methods |
|---|---|---|---|---|---|
| **I** | ~20 km | Taxonomic, functional | Community composition, species richness, alpha diversity (Simpson's index), ecosystem productivity | Local water chemistry, habitat characteristics (sediment, benthic macrofauna, vegetation, amount of stones) | ANOSIM, dbRDA, GLM, hierarchical clustering, PCA, quantile regression models, SEM, SIMPER, species accumulation curves |
| **II** | ~60 km | Taxonomic, functional | Spatial beta diversity (Bray-Curtis, Simpson's and Sørensen's similarity indices) | Local water chemistry, wind exposure | ANOVA, functional trees, GDM, halving distances, LM, random sampling |
| **III** | ~1300 km | Taxonomic | Community composition, species richness | Local water chemistry, climate, spatial variables, wind exposure | GAM, Mantel tests, Moran's *I*, RDA, variation partitioning |
| **IV** | ~2300 km | Taxonomic, functional | Community composition, species richness, spatial beta diversity (Bray-Curtis), temporal beta diversity | Local water chemistry, habitat characteristics (sediment, macrovegetation), climate, spatial variables, wind exposure | GDM, dbRDA, LM, nMDS, pie charts, regression analyses, TBI |
| **V** | 0 km for temporal study, ~50 km for spatio-temporal study | Taxonomic, functional | Community composition, alpha diversity (Shannon's index), temporal beta diversity | Water temperature, air temperature | ANOSIM, ANOVA, nMDS, TBI |

**Diversity-productivity relationship** In paper I, the direct and indirect effects of the environment and taxonomic and functional diversity of communities on ecosystem productivity were analyzed with piecewise structural equation models (SEM; Lefcheck 2019). To represent the environment, PC1 and PC2 axis scores calculated with principal component analysis (PCA) were used, and the alpha diversity

of communities was described with Simpson's diversity index (Simpson 1949). Because the data were heteroscedastic and, thus, not optimal for the SEMs, the relationship between community diversity and ecosystem productivity was also studied with quantile regression models (Koenker & Hallock 2001) using the lower quantile, i.e., fifth percentile. The effectiveness of quantile regressions has been shown in different contexts, such as species distribution modelling (Keeley et al. 2012) and identifying thresholds in ecological interaction networks (Thrush et al. 2012).

**The effect of environment on communities** In papers I, III and IV, the effect of environmental variables on community composition was studied with distance-based redundancy analysis (dbRDA) (I and IV) and redundancy analysis (RDA; Van den Wollenberg 1977) (III). In paper III, variation partitioning (Borcard et al. 1992) was also used to analyze the individual and combined effects of local water chemistry, climate and spatial variables on community composition. In papers I and III, the effect of environment on the diversity of communities was studied using general linear models (GLM) (I) and generalized additive models (GAM; Hastie & Tibshirani 1986) (III).

**Spatial beta diversity** In papers II and IV, linear models were used to analyze the relationship between community similarity/dissimilarity and geographical/environmental distance, and the effect of individual environmental variables on taxonomic and functional beta diversity was studied with generalized dissimilarity modelling (GDM; Ferrier et al. 2007). In paper II, the effect of potential species loss on functional beta diversity was analyzed using all pairwise relationships between community similarity and environmental heterogeneity with randomly sampled (5-95%) subsets of species, and analyzing the difference between subsample sizes with the analysis of variance (ANOVA). In paper III, the Mantel test (Mantel 1967) was used to investigate community turnover along the geographical gradient.

**Temporal beta diversity** In papers IV and V, temporal beta diversity indices (TBI; Winegardner et al. 2017) were calculated to validate the results of the spatial (IV) or temporal (V) sampling. In paper IV the aim was to determine the level of change in communities during the sampling project, and in paper V to compare the degree of change in the communities between the intensively sampled temporal site and the spatio-temporal sites that were sampled only three times.

**Variation in communities along gradients** In papers I, IV and V, samples were divided into groups according to environmental variables. In paper I, the groups were formed using hierarchical clustering (Murtagh 1985) based on significant environmental variables, whereas in paper IV the groups were based on salinity, and in paper V on thermal seasons. Analysis of similarities (ANOSIM) was used in papers I and V to test if the taxonomic and functional composition of communities significantly differed between groups. In paper I, similarity percentages test (SIMPER; Clarke 1993) was also used to calculate the traits that explained most of the variance among the groups, and species accumulation curves to study the observed species richness and estimated total species richness in the groups. In papers IV and V, non-metric multidimensional scaling (nMDS) was used to describe differences in taxonomic and functional community composition among the groups. In paper IV, the results of nMDS were visualized with regression analyses. Finally, in paper V, the significance of overall differences in taxonomic and functional diversity between groups was analyzed with one-way analysis of variance (ANOVA), and the pairwise differences between all groups with Tukey Honest Significant Differences.

# 4. RESULTS AND DISCUSSION

The studies presented in this thesis explored the diversity of benthic diatoms along different gradients and from several perspectives – the effect of diversity on ecosystem productivity (I), the variation in diversity along spatial and temporal gradients (I-V), and environmental factors affecting the diversity (I-IV). The diversity of communities was remarkable in all the datasets, as shown by the species richness, which was 328, 408, 230, 522 and 272 in papers I-V, respectively. Such a high diversity highlights not only the effective adaptation capability and dispersal of microorganisms, but also the usefulness of diatoms in diversity studies in different aquatic ecosystems, including the Baltic Sea, where the challenging salinity conditions and the youth of the basin lead to low overall diversity (Bonsdorff 2006).

The main results of the individual papers are discussed in the following chapters.

## 4.1. Diversity-ecosystem productivity relationship (I)

**Main results** The main objective of paper I was to investigate how the taxonomic and functional diversity of benthic diatom communities affects the productivity of the ecosystem. The SEMs that used average responses explained only 15% of productivity, and the link between diversity and productivity was significant only for the functional diversity, and nonsignificant for the taxonomic diversity. The quantile regression models with the lower quantile, i.e., fifth percentile, were considerably better fitted to the data (Fig. 4). Both taxonomic and functional diversity had significant lower quantile relationships with productivity, but the model with functional diversity was better fitted and, thus, explained ecosystem productivity more effectively.

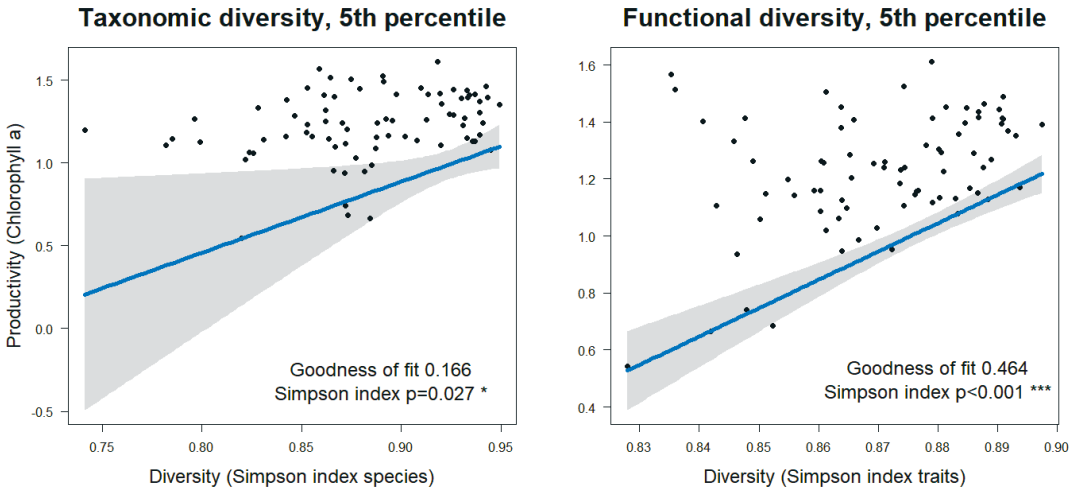


Fig. 4. Quantile regression models showing the 5$^{th}$ percentile relationship between diatom diversity (Simpson's Diversity Index) and ecosystem productivity (Chlorophyll *a*). The left panel represents taxonomic diversity, and the right panel functional diversity. < 0.001 ***, < 0.01 **, < 0.05 *

**Lower boundary relationship** The results suggested that the diversity of benthic diatom communities is important for the functioning of ecosystems and may set the lower boundary for benthic ecosystem productivity. Thus, productivity can be high even when the diatom diversity is low, but high diversity

seems to support high productivity. Despite the considerable amount of research on diversity-productivity relationships conducted in different environments and ecosystems (e.g., Tilman et al. 1996; Paquette and Messier 2011), this was likely the first study to show such a lower boundary relationship. However, comparisons are hindered by the lack of corresponding studies, because the effect of the diversity of benthic diatoms on the functioning of marine or brackish ecosystems has, so far, been poorly studied. The significant lower boundary relationship may have referred to a phenomenon called 'factor ceiling' (Thomson et al. 1996; Cade et al. 1999), which is a useful theory particularly for ecological datasets, where data points are typically widely scattered around the average regression but often effectively limited by an upper or lower limit. It indicates that despite several factors possibly affecting the response variable – in this case ecosystem productivity –, the extreme limit is controlled by the variable of interest – in this case diatom diversity (Thomson et al. 1996). Thus, in the ecosystem studied here, other factors, such as habitat characteristics, benthic macrofauna, and nutrient concentrations, may have been involved in affecting the benthic productivity, but the lower limit of productivity was likely controlled by the diversity of diatom communities.

**Environmental heterogeneity** Some samples with low diversity had high productivity, and this may have been due to the presence of some species with high biomass production capability (Aarssen 1997), or the contribution of other microphytobenthic organisms, mainly cyanobacteria (Watermann et al. 1999). A major source for the large variation in the diversity-productivity relationship between samples may also have been the heterogeneity of the environment. This has also been shown by Gustafsson & Norkko (2019) and Gammal et al. (2019), who concluded that the environmental context is crucial in mediating the benthic diversity-ecosystem functioning relationships. Thus, to understand how the diversity of communities affects ecosystem functions and services, more field studies in naturally complex ecosystems are needed (see also Snelgrove et al. 2014).

**Functional diversity** The results also clearly illustrated that the functional diversity of communities was more effective than the taxonomic diversity in showing the relationship between diversity and ecosystem productivity. Although a large part of studies still concentrate on the taxonomic composition of communities and the importance of species identities in ecosystem studies has also been highlighted (Gammal 2019), functional traits have repeatedly been shown to be robust indicators of ecological behaviour (Westoby et al. 2002) and, thus, related to ecosystem functioning (Roscher et al. 2012; Gustafsson & Norkko 2019). The effectiveness of functional diversity to explain ecosystem productivity can be due to many reasons that are more thoroughly discussed in the introduction of this thesis. This study being an observational investigation, the main reason for the positive diversity-productivity relationship or the superiority of functional diversity over taxonomic diversity in showing this relationship could not be determined. However, the results presented here highlight the usefulness of functional traits in diversity-productivity research.

**Conclusions** Overall, the diversity of benthic diatoms seemed to affect ecosystem functioning by setting the lower limit to productivity, and the functional diversity of communities was more effective than the taxonomic diversity in showing this relationship. However, to determine the generality of these patterns, more research in naturally complex ecosystems is needed.

### 4.2. Spatial beta diversity along environmental and spatial gradients (II, III and IV)

**Main results** Spatial beta diversity, i.e., the change in community composition between sites, along environmental and spatial gradients was studied in papers II, III and IV. Across all geographical scales, the change in the environmental conditions led to high taxonomic beta diversity (Fig. 5). This was indicated by the significant correlation between community dissimilarity and geographical distance

(III), and the maximum values of Bray-Curtis dissimilarity index (II: 0.956, IV: 0.990). Instead, the functional beta diversity remained considerably lower (maximum values of Bray-Curtis dissimilarity index in paper II: 0.342, in paper IV: 0.577) (Fig. 5). Simulated species loss significantly increased the degree of functional beta diversity, when more than 50% of the species in the communities were randomly removed (II). At the small geographical scale (II), the taxonomic beta diversity was mostly explained by wind exposure, salinity and temperature, and the functional beta diversity by temperature. At the large geographical scale (IV), salinity, climate and spatial factors mostly explained both taxonomic and functional beta diversity.

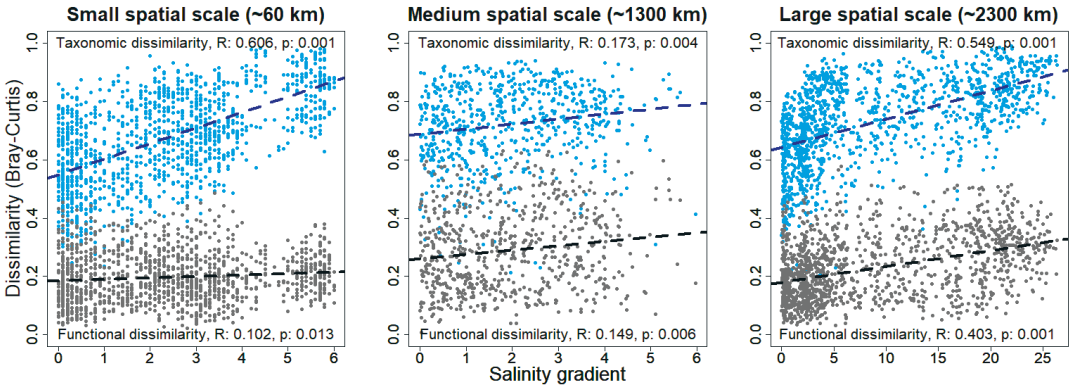


Fig. 5. Pairwise relationships between taxonomic/functional dissimilarities (Bray-Curtis dissimilarity index, abundance data) and the salinity gradient at small, medium and large spatial scales. Blue dots and lines represent taxonomic dissimilarity, and gray dots and black lines functional dissimilarity. Dashed lines denote linear models fitted to data, and the goodness of fit values for linear models are indicated by Mantel R and p values. To enable comparison in the thesis summary, the corresponding analysis was run also for the medium geographical scale study (III), although this analysis was not included in the original paper.

**General pattern of high taxonomic but low functional beta diversity** The difference in spatial scale between papers II (~60 km), III (~1300 km) and IV (~2300 km) did not affect the finding of high taxonomic but low functional beta diversity along the study gradient. Thus, as the environmental conditions varied along the gradient, species were replaced by taxonomically different but functionally fairly similar species. High taxonomic beta diversity has been commonly found in regions with dispersal barriers (Fiera et al. 2018), and low functional despite high taxonomic beta diversity at small spatial scales with strong environmental gradients, such as estuaries (Villéger et al. 2012). However, the results of high taxonomic but low functional beta diversity, shown at different spatial scales here, were able to indicate the generality of the pattern, which has been poorly studied so far. It seems that the requirements for the functional characteristics of microphytobenthos to maintain stable benthic ecosystem functioning are quite similar in different environments, and that diatoms are able to meet these requirements despite high environmental variability. To further improve the generality of this result, the possible confounding effect of the difference in the number of species (average 55 per sample) and traits (6 per sample) was accounted for by calculating the taxonomic beta diversity with only dominant species and with randomly sampled subsets of species (II). The result still remained the same.

**The effect of species loss** Such a high functional similarity of communities despite strong environmental variation and low taxonomic similarity may indicate that diatoms, and possibly microorganisms in general, provide an insurance effect against environmental change. However, if the environmental change is strong enough to lead to severe species loss, the insurance effect may be lost (II). With environmental change, relative proportions of different primary producers, such as diatoms, cyanobacteria, green algae and dinoflagellates, may also change in communities (Hinder et al. 2012). The effects of environmental change on the functional composition of communities have been studied before with macro-organisms, such as benthic marine communities exposed to ocean acidification (Teixidó et al. 2018) and coral reef fishes vulnerable to fishing (D'agata et al. 2016), but the effect of species loss on the functional composition of communities is poorly known and difficult to study in natural systems. The method used here, i.e., statistically simulating species loss by using randomly sampled subsets of species, is not perfect either, as it fails to consider biotic interactions and differences in species' sensitivity to environmental change. However, these factors are largely unresolved for microorganismal communities and, thus, could not be included in the model. The finding of decreasing functional similarity with species loss indicated that some of the unique functional traits may disappear from communities, if the taxonomic diversity decreases. In the benthic diatom communities studied here, rare functional traits included the large-sized, colonial, low-profile and nitrogen-fixer diatoms. The disappearance of these traits would possibly lead to changes in how the communities are able to acquire nutrients (Snoeijs et al. 2002) and resist disturbance (Passy 2007), which may affect the overall productivity and performance of the communities.

**The effect of environment on beta diversity** The environment explained 61.4% (II) and 52.5% (IV) of the deviance in taxonomic beta diversity. Although even higher explained deviances have been found for some macroorganisms (Heino et al. 2019; beta diversity of beetles), these values are high compared to the explained deviance of the beta diversity of many other organisms, such as amphibians (Valdujo et al. 2013; 44%), macroalgae (Leaper et al. 2011; 36%), and macroinvertebrates (Nieto et al. 2017; 33%). Such high values were astonishing, given that the communities of microorganisms, such as diatoms, consist of a high proportion of rare species, which may lead to the relatively low ability of the environment to explain the taxonomic composition (Heino et al. 2010; Pajunen et al. 2016). The high explanatory power of the models was probably due to the clear environmental gradients from freshwater to brackish (II) and from freshwater to marine waters (IV) used in the studies. As expected, the salinity gradient was an important driver for the taxonomic community composition. The strong effect of salinity on the communities of diatoms (Snoeijs 1995) and other aquatic organisms (Cognetti & Maltagliati 2000; Ysebaert et al. 2003) has been widely discovered. As described by the Remane curve (Remane 1934), most of the organisms are adapted to either freshwater or marine realms and adaptation to the brackish environment is difficult, which leads to a dramatic change in the composition and richness of communities along the salinity gradient. The effect of salinity was accompanied by wind exposure, water temperature (II) and climate (IV), all of which formed clear gradients along the study areas. Surprisingly, the environment was less effective in explaining the functional beta diversity, as suggested by only 15.8% (II) and 28.2% (IV) of deviance explained by the GDMs. Thus, the functional composition of communities was more robust to the variations in the environment. This may be due to the robustness of the functional composition to water chemical factors, such as salinity (Passy 2007). However, given that the functional composition of diatom communities is usually closely related to disturbances (Passy 2007), the low explained deviance despite the strong wind exposure gradient was surprising (II).

**Conclusions** Overall, results presented in papers II, III and IV suggested that benthic diatom communities along strong environmental gradients are functionally fairly similar despite high taxonomic beta diversity, and this pattern applies across all spatial scales. The importance of biodiversity was also emphasized, because although the high functional similarity may provide resilience against environmental change, it seems to be threatened by species loss.

### 4.3. The effect of environment on communities at different environmental and spatial gradients (I, III and IV)

**Main results** The effect of environmental variables on the variation of local communities was investigated in papers I, III and IV. Significant environmental drivers for the communities varied between studies (Fig. 6), thus emphasizing the effect of regional differences and spatial observation scale on the results of ecological research. The taxonomic community composition was controlled by nutrients ($NO_2^-$, $NO_2^- + NO_3^-$, $NH_4^+$, $PO_4^{3-}$, total P, and/or silicate) in all papers. In paper I, where samples were collected from sedimentary soft bottoms on a small spatial scale, sediment organic matter content had a strong effect on the taxonomic community composition, whereas in papers III and IV, where samples were collected from stones on larger spatial scales, significant variables included air temperature (III), water temperature (III and IV), salinity (III and IV), wind exposure (IV), amount of sediment on the bottom (IV), and sampling stone volume (IV). The functional community composition was significantly affected only by sediment organic matter content in paper I, and the combination of $PO_4^{3-}$, wind exposure, stone volume, and pH in the different parts of the gradient in paper IV. In paper III, species richness was controlled by pH, total P and total N, whereas in paper I, the Simpson's index for taxonomic and functional diversity was mainly controlled by habitat characteristics, namely vegetation cover, and the organic matter content, grain size and mud content of the sediment.

**Nutrients** Nutrients have frequently been reported as drivers of microphytobenthic communities (Passy 2007; Lange et al. 2011). Different geographical areas can be limited by different nutrients (Soininen 2009), which was also shown in paper IV, where nutrient limitation varied along the large spatial gradient. Production in freshwaters and the low saline parts of the Baltic Sea is usually limited by P (Schindler 1974), and production in marine and brackish waters, such as the majority of the Baltic Sea basin, by N (Nixon et al. 1996; Tamminen & Andersen 2007). This pattern was partly supported by the studies presented in this thesis (IV), although the joint limitation of N and P was also found (III and IV). Deviance from the general pattern may have been due to, e.g., seasonally varying nutrient concentrations or the effect of eutrophication (Tamminen & Andersen 2007).

**Gradients of salinity and temperature** Due to the strong freshwater-brackish-marine and climatic gradients in papers III and IV and in the Baltic Sea in general, the often strongly inter-correlating factors representing this gradient, namely salinity, water temperature, air temperature and precipitation, were central for the composition and diversity of diatom communities. The intermediate salinities of 5-6 are the tipping point for the biotic communities (Remane 1934) and, thus, the importance of salinity as a driver for communities depends on the length of the study gradient. Studies with short salinity gradients (e.g., Weckström & Juggins 2005, salinity gradient 0.7-6.4) have reported no effect of salinity, whereas studies with long salinity gradients (e.g., Ulanova et al. 2009, salinity gradient 0.4-11.4; Clarke et al. 2003, salinity gradient 2.7-31.1) have identified salinity as a major driver for the communities. The previous results on the effect of temperature on diatom communities are less coherent, as some studies have found a strong temperature effect (Passy et al. 2018; Yu et al. 2019), whereas others have reported the opposite (Soininen 2007). This difference in results may stem from

the high correlation of temperature with several measured or unmeasured variables, such as biotic interactions, water flow, or light intensity.

**Habitat characteristics** The effect of habitat characteristics and heterogeneity on the diversity of macro-organisms has been studied extensively (e.g. Tews et al. 2004), and the habitat and the environmental setting has been shown to directly and indirectly affect the biodiversity-ecosystem functioning relationships (Gammal et al. 2019). Considering the importance of the habitat, it is surprising how rarely such characteristics are considered in microphytobenthic studies. Paper I showed that the habitat characteristics, such as sediment grain size, organic matter content and macrovegetation cover, overrode all other environmental variables as drivers of diatom diversity. In paper IV, the effect of habitat was not as preeminent, but the amount of adjacent sediment still affected diatom community composition on stones. The roles of sediment characteristics as drivers of diatom communities can be diverse. Small grain size sediments and the presence of sediment on stones may increase diatom diversity by enlarging the surface area of the substratum, by providing high organic matter content for the nutrition of diatoms (Rusch et al. 2003), or by decreasing the abundance of grazers (Hall & Anderson 2013). Results presented here suggested that the habitat characteristics can provide substantial study gradients and should more often be considered in studies on microphytobenthic communities. Ignoring habitat gradients may possibly lead to low explained deviances, such as in paper III of this thesis and many other diatom studies.

**Disturbances and biotic interactions** The effect of disturbances and biotic interactions on diatom communities has also often been ignored, possibly due to difficulties in measuring them and the complexity of interactions. In paper III, the effect of wave inducing wind exposure was not significant for the communities, but this may be due to the measuring/interpolating method, which has been found to be unsuitable for the complex archipelago of the northern Baltic Sea. In contrast, the disturbance by wind exposure was measured with a more appropriate method and found significant in paper IV, which agrees with the few previous studies that have considered the effect of wind or waves on diatoms (e.g., Busse & Snoeijs 2003; Ulanova & Snoeijs 2006). Biotic interactions between diatoms and benthic fauna were considered in paper I. The abundance of benthic fauna was found to increase along the sediment grain size gradient, and to correlate with the abundance of diatom species that grow in a low position, attached to the substrate. This indicates that grazers consume the high-positioned diatoms, thus affecting the structure of the microphytobenthic communities (Jyrkänkallio-Mikkola et al. 2016). The inclusion of benthic fauna as a driver for the diatom communities was not possible in paper IV, but due to the increase of the species richness, abundance and the size of individuals of benthic fauna along the study gradient towards marine conditions (Norkko et al. 2015), it may have improved the results.

**Spatial gradients** Spatial gradients are typically hard to distinguish from the environmental gradients in all kinds of ecosystems, and especially in the Baltic Sea due to high correlations between North-South and East-West spatial gradients, climate, and local water chemistry, particularly salinity. The spatial effect may also be less significant in marine environments with free water flow between study sites and consequent unlimited dispersal, than in freshwater or terrestrial systems with stronger dispersal limitation (Potapova & Charles 2002; Freestone & Inouye 2006). However, the importance of the extent of the study gradient, either environmental or spatial, was clearly shown in papers I and IV. In paper I, the large sedimentary gradient, from muddy sites with small grain size and high organic matter content to sandy sites with large grain size and low organic matter content, enabled the observation of the diversity pattern of diatom communities related to the environmental gradient, i.e., higher diversity at sites with small grain size sediments. In paper IV, the large gradient of inter-correlated salinity, climate and spatial variables allowed the recognition of the gradual change in the

functional composition of the communities along the gradient, i.e., the increase of large, colonial and high-positioned species towards low salinities, and the differentiation of the significant environmental variables at different parts of the gradient.

**Conclusions** The effect of environmental variables on biotic communities has been widely studied. However, previous studies and papers in this thesis have shown that general patterns are difficult to find, as the effect of environment seems to be context-dependent and variable between regions. This emphasizes the need to consider region-specific differences in, e.g., environmental management and conservation efforts.

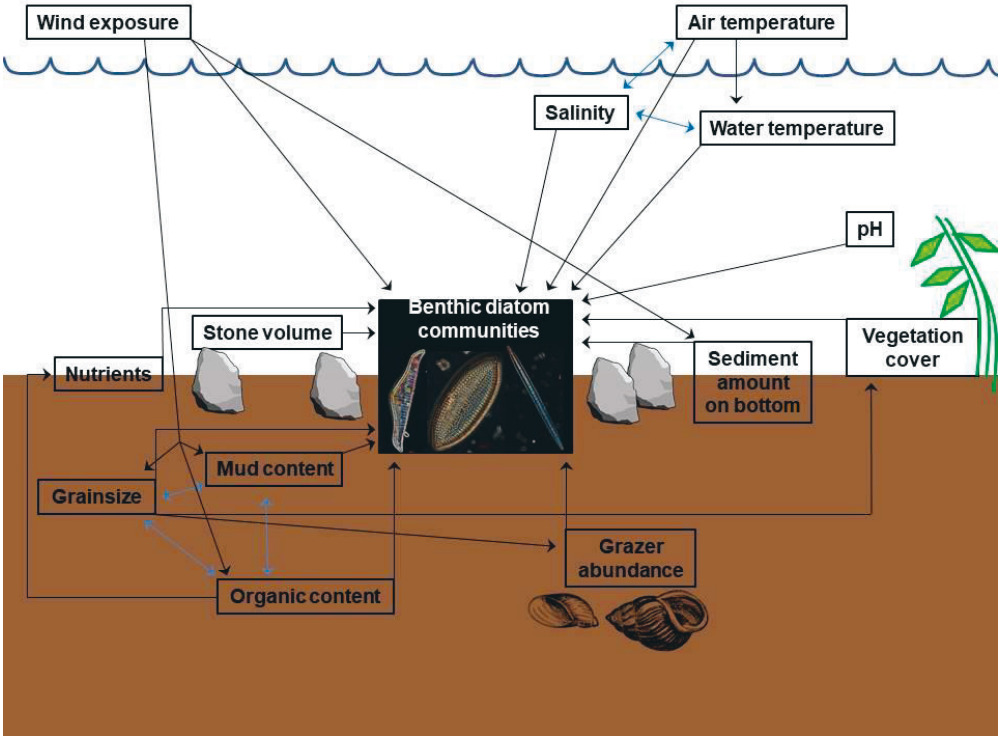


Fig. 6. Environmental variables that affected the diversity and composition of benthic diatom communities in different studies of this thesis. The model only lists variables considered in the present studies. Black arrowheads denote direct effects, and blue arrowheads denote strong inter-correlation without a clear causality.

### 4.4. Variation in communities along a seasonal and inter-annual temporal gradient (V)

**Main results** The aim of paper V was to investigate seasonal and inter-annual variation in the taxonomic and functional community composition and alpha diversity of benthic diatom communities. This was important for the purpose of increasing knowledge on temporal variation in communities that has been studied less than the spatial variation, but also for the purpose of validating the results of the spatial snapshot studies of this thesis. The taxonomic and functional community composition varied considerably among most of the seasons and also between the first and the second sampling year. The

seasonal variation for both taxonomic and functional composition was cyclic along the course of the year, but the taxonomic composition cycles were clearly different between years, whereas the functional composition cycles were more similar between years. Despite the clear seasonal variation in community composition, the alpha diversity remained fairly stable throughout the sampling period. However, the climatically very different winters seemed to affect the diversity of communities, since the highest alpha diversity was found during the cold winter with long-lasting ice-cover, and the lowest diversity during the mild winter with a short ice-cover period.


Fig. 7. The temporal sampling site during different seasons: a) fall, b) winter, c) spring, and d) summer. The photographs demonstrate the strong seasonal variation of climate at the sampling site.

**Variation in taxonomic community composition** The high variation in the taxonomic community composition along the temporal gradient was expected because of the high seasonal variation of environmental conditions in the sampling area (Fig. 7), and because of similar results found with different organisms, such as soil microbes (Waldrop & Firestone 2006), bacterioplankton (Van der Gucht et al. 2001) and fishes (Lazzari et al. 1999). Comparisons to microphytobenthic organisms in the Baltic Sea are hindered by the lack of previous studies with temporally extensive datasets. Sabbe (1993) and Vilbaste et al. (2000) have studied the temporal variation of benthic diatoms in a brackish Westerschelde estuary in the North Sea, and the Gulf of Riga in the Baltic Sea, respectively, and found temporally stable community compositions, but their temporal gradients were considerably shorter than

the one in the study presented here, and they collected samples from sedimentary soft bottoms, which may form temporally more stable substrata for biotic communities than stones that were used here. High seasonal and inter-annual variation in the taxonomic composition, which was found here, indicates that different species have quite narrow environmental optimums and tolerances (Soininen 2007).

**Variation in functional community composition** Instead, the high seasonal variation in the functional composition of communities along the temporal gradient was surprising, because on spatial gradients, the functional variation of benthic diatoms is often low despite highly variable environments and taxonomic composition (see chapter 4.2). However, this finding of high variation in functional composition agrees with Soininen et al. (2016), who showed that the functional composition of diatom communities is efficient in detecting environmental gradients, and with Passy (2007), who showed that different functional groups of benthic diatoms respond differently to environmental conditions.

**Variation in alpha diversity** Despite high seasonal variation in the community composition, variation in alpha diversity was low. Such a general pattern has been shown also before in the Baltic Sea (Sabbe 1993; Vilbaste et al. 2000). However, it disagrees with studies conducted in other ecosystems, such as deep sea (Ramalho et al. 2014), pelagic waters (Sabanci & Koray 2011), and terrestrial ecosystems (Smith et al. 2018), where the diversity changed significantly between seasons and years. Low variation in alpha diversity despite considerable changes in the community composition refers to either an ample seed bank, i.e., locally occurring resting stages of species, or a large regional species pool and effective dispersal of species (Zobel 1997). Both of these alternative mechanisms would lead to the effective replacement of species that disappear temporarily due to seasonal environmental changes. Although the results of this study could not detect seasonal variation in ecosystem functioning, it can be speculated that the temporally stable alpha diversity of diatom communities may allow ecosystem stability and provide resilience against environmental change (Naeem et al. 2012).

**The effect of ice-cover** However, the alpha diversity of communities was significantly lowest during the mild winter, when ice-cover duration was short. During this winter, small and mobile (featuring traits small-sized, mobile, non-colonial and motile) species formed proportionally large parts of the functional communities, whereas during the cold winter with long-lasting ice-cover diversity was high, and large (featuring traits large-sized, pedunculate, pad-attached, colonial, and high-profile) species were more dominant. The results of this study cannot detect the fundamental reason for these differences, but it can be speculated that, at high latitudes, the conditions during winter are always harsh due to the cold temperatures, and in order to maintain high diversity, the microphytobenthic communities require a stable ice-cover to protect them from wind and wave induced disturbances (Morin et al. 2014). This theory is supported by Passy (2007), who showed that high-profile diatom species cannot tolerate high disturbances, and by Busse & Snoeijs (2002) who indicated that small and large diatom species are affected differently by wave action. Only two winters were included in the study presented here and, thus, caution is needed in the interpretation of the consequences of the seasonal diversity changes. Furthermore, the total abundances of different species or the whole communities that have previously been shown to vary temporally (Joensuu et al. 2020) were not considered here. However, these results may indicate that the climate change that is expected to raise temperatures and shorten the annual ice-cover period at high latitudes will reduce the winter diversity of microphytobenthic communities in the future, which may affect the functioning of the benthic ecosystem.

**Conclusions** Despite considerable seasonal and inter-annual climatic variation in a large part of the globe, changes in biotic communities along the course of seasons and years have been understudied. This is understandable, because the consideration of such a variation requires temporally long datasets that are difficult to collect, especially in areas where the ice-cover sets an annual challenge. The results presented here indicate a strong seasonal climate-induced variation in the microphytobenthic communities, suggesting that considering temporal variation is crucial for the monitoring and conservation efforts of coastal ecosystems.

# 5. CONCLUSIONS AND FUTURE PERSPECTIVES

The overall aim of this thesis was to explore either generalizable or variable patterns of taxonomic and functional diversity along different spatial, environmental and temporal gradients, and to analyze the effect of the diversity of benthic diatom communities on ecosystem functioning. Several aspects considered here, namely the gradient approach in biodiversity research, the functional diversity of communities, and the effect of microorganismal diversity on ecosystems, have previously been understudied.

When considering the generality or variability of diversity patterns along different gradients, general patterns were found in

a) the spatial beta diversity of communities, as at all spatial scales the strong environmental gradient resulted in high taxonomic beta diversity, i.e., the majority of species changing along the gradient, but the functional beta diversity remained considerably lower. This may indicate that, in order to maintain stability in ecosystem functioning, the functional requirements for the benthic microorganismal communities are fairly similar across very different ecosystems with contrasting environmental conditions;

b) the temporal variation in the alpha diversity of communities, which was fairly stable despite strong seasonal and inter-annual variation in climate. The temporally stable diversity may allow ecosystem stability and resilience against environmental change.

Variable patterns were found in

c) environmental factors affecting the diversity and composition of communities within and between gradients and regions. Similar results of varying environmental drivers in different ecosystems have been found commonly in microorganismal diversity research (Teittinen 2019 for diatoms; Shan et al. 2019 for cyanobacteria). This emphasizes the need to consider region-specific differences in modelling and conservation efforts of ecosystems;

d) the temporal variation in the taxonomic and functional composition of communities, which varied between seasons and years. This suggests that caution should be taken in research, modelling or environmental management programs that combine datasets from different time periods.

The results of this thesis also suggested that despite the high variation of diversity in natural ecosystems, the diversity, especially functional diversity, of benthic diatoms affects the functioning of the ecosystem by setting the lower limit to productivity. This finding has several implications for larger purposes, such as efforts to understand the large-scale functioning of ecosystems, or ecosystem modelling that is largely used for simulating ecosystems and as a tool for ecosystem management. First of all, the effect of pelagic microorganisms is usually included in the models assessing, e.g., nutrient cycles or eutrophication in aquatic systems (e.g., Undeman et al. 2014; the BALTSEM model), whereas benthic microorganisms are often neglected. According to the results of this thesis, it would be important in the future to also consider the effect of benthic microorganismal communities. Secondly,

the functional approach, such as using functional diversity measures in addition to taxonomic diversity, has several advantages and is highly recommended for future studies. It can demonstrate relationships that would otherwise remain hidden, and it can provide ecological conclusions that are transferrable to ecosystems with taxonomically different species (Villéger et al. 2012). Thirdly, interactions in natural ecosystems are complex and context-dependent, which may result in noisy relationships and difficulties in the interpretation of the models. Thus, careful inspection of the data and the consideration of models suitable for addressing other kinds than average responses are recommended. And fourthly, the diversity of benthic communities in coastal ecosystems seems to be highly variable and patchy, which sets a challenge to model building and predictions, but should be considered when managing these valuable ecosystems.

Due to the interesting diversity-ecosystem productivity relationship found with benthic diatoms on sedimentary substrata (I), the next step would be to consider the abundances of benthic diatom communities and the relationship between diatom communities and ecosystem functions in different habitats. Although the importance of microphytobenthic organisms for ecosystem functions has been recognized, it is largely overlooked (Hope et al. 2019) and deserves much more attention, especially at the current times of fast human-induced environmental change.

Finally, to conclude the results of this thesis, a meta-analysis (Fig. 8) based on the spatial gradients in studies I-IV was built to show the effect of observation scale on the obtained results of diversity. The meta-analysis indicated that increasing the spatial study scale may allow the observation of a more representative sample of the diversity, but this relationship is not strictly linear and is highly dependent on the environmental gradient of the study. Thus, when drawing conclusions on the effect of spatial gradients on ecological measures, such as biodiversity, it should be noted that natural gradients are induced by the combined effects of numerous biotic and abiotic factors (Huston 1994), and more research of natural ecosystems is needed to resolve biodiversity patterns in the rapidly changing world.

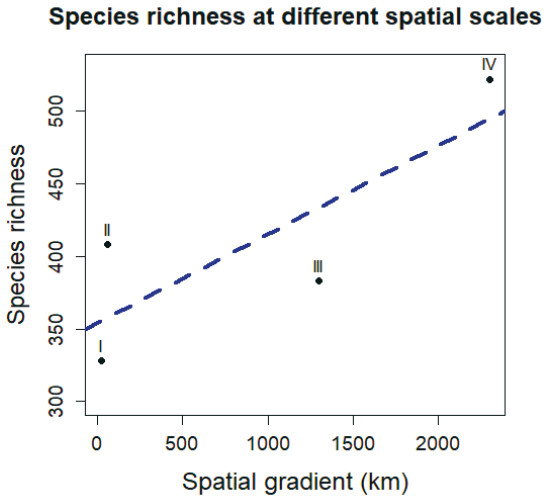


Fig. 8. The observed species richness of papers I-IV along the spatial gradient of the studies. The dashed line denotes linear model fitted to data. The meta-analysis aims at qualitatively showing the relationship without indicating the goodness of fit or significance of the model, because the strict comparison of the different datasets is complicated by different numbers of samples and identified frustules in studies (300 in III vs. 500 in I, II and IV). The latter was corrected by multiplying the species richness of paper III by 5/3. This correction method was considered best here, although the increase of species richness may not always increase linearly with increasing number of identified frustules.

## 6. ACKNOWLEDGEMENTS

First of all, I want to thank my supervisors Prof. Janne Soininen and Prof. Alf Norkko, who have made this project possible.
Janne, thank you for taking the initiative to help me to get started with this project, and for your useful advice along the way.
Alf, my sincere thanks for all your help, support and encouragement. I am deeply grateful for all the discussions, about science of course, but especially about life in general.

I am very thankful for my opponent Prof. Pauline Snoeijs Leijonmalm for discussing my work. Sincere thanks also to the pre-examiners Prof. Veijo Jormalainen and Prof. Kalle Olli for the time that you dedicated into examining my thesis.

This work was conducted at the Department of Geosciences and Geography, University of Helsinki, and Tvärminne Zoological Station, University of Helsinki. Thank you for providing excellent facilities and an inspiring atmosphere for working. I am grateful for the Walter and Andrée de Nottbeck Foundation that provided the major part of funding for this project, and for the Finnish Society of Sciences and Letters, Societas pro Fauna et Flora Fennica, and the University of Helsinki for their travel grants.

I have had the privilege to work in two research groups. I would like to thank the members of our group at Kumpula campus, especially Anette Teittinen – we have shared a lot of fun moments both in the field and in the lab. I am grateful to the wonderful Tvärminne Benthic Ecology Team – Johanna Gammal, Anna Villnäs, Saara Mäkelin, Iván Rodil, Camilla Gustafsson, Mari Joensuu, Laura Kauppi, Charlotte Angove, Mats Westerbom, Tuomas Kahma and Norman Goebeler – for welcoming me to the group. The whole project would have been totally boring without all of you!

My sincere thanks go to the lovely people at the Tvärminne Zoological Station. I would like to thank Dr. Joanna Norkko for welcoming me to the station and making me feel like home from the very beginning. I am also grateful for Mervi Sjöblom, Jaana Koistinen, Noora Haavisto, Hanna Halonen, Jostein Solbakken, Minna Österlund, Mariella Holstein-Myllyoja, Anu Vehmaa, Göran Lundberg and the trainees for all the support during different stages of this project. And my special thanks go to Tapio Rautalin – my winter sampling would not have been possible without you and your chainsaw!

I have been fortunate enough to receive help from several other people during this project. I would like to thank Judi Hewitt, Aleksandra Lewandowska and Caio Graco-Roza for support with statistics, Paloma Lucena Moya for help with GIS, Elina Leskinen for making all the practical things so easy, Juhani Virkanen, Hanna Reijola and Tuija Vaahtojärvi for help in the lab, and Kaarina Weckström for sharing your diatom identification knowledge and literature. I am also grateful for my co-authors Guillaume Bernard and Marie Järnström for your contribution.

Last but definitely not least, I want to thank my family, also my dad who showed me how beautiful the Baltic Sea is – I think he would be proud of my achievement.

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